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Change of Homozygote Excess during Growth in the Japanese Scallop, *Patinopecten yessoensis*

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Summary

Observed and expected heterozygosity at the twelve isozyme loci was analyzed in comparison with shell length of several lots of the Japanese scallop (*Patinopecten yessoensis*). In some of the loci the observed heterozygosity (Ho) was significantly lower than the expected heterozygosity (He) in the small size lots, indicating an excess of homozygosity, while such tendency was not observed in the large size lots. A positive correlation was observed between the *d* value measured by (Ho-He)/He and the shell length. Thus, there is considerable evidence for heterotic effect during growth.

The Japanese scallop (*Patinopecten yessoensis*) has been cultured in the area of Hokkaido and northeast Honshu in Japan. The seeds for the culturists are obtained through collection of larvae from the sea. The origin of these larvae is not only from natural populations but also from artificial sown and cultured populations, because the collection area lies near the mass culture area.

After techniques of mass culture are established, then improvement of the scallop quality is required. To improve the quality, selective breeding is necessary. Selection is defined as the process that will determine the related individuals allowed to belong to different genotypes.

By using isozyme genes, Kijima *et al.* (1, 2) indicated the high genetic variability and low genetic differentiation in the Japanese scallop populations. Oniwa *et al.* (3) demonstrated a positive correlation of genetic variability (average heterozygosity of isozyme gene) with coefficient of variance of whole body weight (BW), soft part weight (SW) and SW/BW, suggesting the existence of genetic variation in the quantitative traits.

The purpose of the study is to estimate genetic variability in the Japanese scallop based on isozyme genes and to determine whether or not a relation exists between the isozymic genotypes and the size.

Materials and Methods

Table 1 shows the sampling location and shell length of the Japanese scallop examined in the present study. Of the 37 lots, six are seeds (S1-S6), seven are cultured individuals (C1-C7), and 24 are released and natural individuals (RN1-RN24). The seeds are originated from natural larvae, which were collected in May and July from coastal areas and cultured in the sea.

Isozymes were detected using starch gel electrophoresis and the 12 loci were analyzed. Most isozyme data were obtained from the data of Kijima *et al.* (1, 2) and Fujio and von Brand (4). Additional data are S4, S6, C3, C4, C5, C6, C7, and RN17. The degree of allelic fluctuation among lots was measured by Wright's Fst which is equal to $\sigma^2/p(1-p)$, where σ^2 is the observed variance of allele frequencies among lots and p is the average allele frequency of the lots.

For the estimate of genetic variation, the observed heterozygosity (Ho) was calculated from direct count of heterozygotes and the expected heterozygosity (He) was calculated from the allele frequencies ($he=1-\Sigma q i^2$ and $q i$ is the frequency of the ith allele). The excess of homozygotes from the expected, under Hardy-Weinberg's equilibrium, was measured as $d=(Ho-He)/He$. A negative value indicates an excess of homozygotes and a positive value an excess of heterozygotes.

Results

Distribution of Genetic Variants

Twelve isozyme loci were examined in 37 lots of the Japanese scallop as shown in Table 2. At the *Aat-1* locus, four alleles were detected and the *B* allele was dominant. The frequency of *B* allele ranged from 0.618 to 0.880 with a mean of 0.769 and the Fst was 0.027. At the *αGpd* locus, five alleles were detected and the *B* and *C* alleles appeared most dominantly. The frequency of *B* allele ranged from 0.330 to 0.650 with a mean of 0.467 and Fst was 0.027. At the *Gpi* locus, four alleles were detected and *C* allele was dominant. The frequency of *C* allele ranged from 0.743 to 0.970 with a mean of 0.855 and the Fst was 0.018. At the *Pgm-1* locus, seven alleles were detected and the *C* and *D* alleles appeared most dominantly. The frequency of *D* allele ranged from 0.444 to 0.697 with a mean of 0.579 and Fst was 0.016. These four loci showed polymorphism in all lots. Polymorphism was identified as the frequency of the common allele was less than 0.95.

At the *Idh-2* locus, three alleles were detected and the *A* allele was dominant. The frequency of *A* allele ranged from 0.895 to 0.967 with a mean of 0.933 and the Fst was 0.009. At the *Sod-3* locus, four alleles were detected and the *B* allele was dominant. The frequency of *B* allele ranged from 0.601 to 1.000 with a mean of

TABLE 1 *Data of Specimens used in the Present Study*

Lot	Locality	Collection Date	No. of Individuals	Age (Year)	Shell Length Mean(cm)±SD
Seed					
S1	Abashiri	1983.6	121	1	3.30±0.43
S2	Abashiri	84.6	99	1	3.47±0.39
S3	Abashiri	87.7	116	1	4.26±0.57
S4	Abashiri	90.12	120	0.5	2.45±0.36
S5	Rausu	84.6	99	1	3.22±0.38
S6	Mutsu Bay	94.10	100	0.5	2.16±0.26
Cultured					
C1	Lake Saroma	82.9	56	3.5	10.74±0.54
C2	Lake Saroma	82.9	59	3.5	8.63±0.61
C3	Mutsu Bay	94.6	61	1	7.84±0.45
C4	Mutsz Bay	94.6	104	1	8.17±0.46
C5	Mutsu May	95.5	100	1	7.44±0.46
C6	Mutsu Bay	95.5	100	1	7.47±0.55
C7	Ohfunato	95.5	100		12.43±0.67
Released and Natural					
RN1	Sarufutsu	82.9	60		14.66±0.95
RN2	Yuhbetsu	82.8	60	5～7	12.01±0.90
RN3	Tokoro	87.9	99		12.86±0.63
RN4	Lake Notori	82.10	60		13.94±0.86
RN5	Abashiri	82.4	100	2	7.50±0.49
RN6	Abashiri	82.4	112	8	8.84±0.59
RN7	Abashiri	82.4	98		13.69±0.69
RN8	Abashiri	82.4	100	4	10.83±0.62
RN9	Abashiri	82.8	60		14.60±0.77
RN10	Abashiri	82.9	60		8.43±0.45
RN11	Abashiri	82.10	60	3.5	9.18±0.63
RN12	Abashiri	84.7	100	3	8.57±0.69
RN13	Abashiri	84.7	100	3	9.29±0.46
RN14	Abashiri	84.8	125	2	7.26±0.63
RN15	Abashiri	84.8	96		10.40±0.70
RN16	Abashiri	89.11	48	4	10.47±0.80
RN17	Abashiri	90.9	100	1.5	4.68±0.31
RN18	Notsuke	82.10	30		13.77±1.80
RN19	Akkeshi	88.2	100		11.14±0.80
RN20	Funka Bay	88.2	100		10.35±0.51
RN21	Mutsu Bay	87.9	99		12.07±0.76
RN22	Ohfunato	87.12	100		11.79±1.04
RN23	Kesennuma	87.10	100		11.45±1.06
RN24	Souma	87.11	100		14.02±0.67

TABLE 2 *Common Allelic Frequencies at the 12 Loci in Japanese Scallop*

Lot	Locus and Allele											
	Aat-1 B	*αGpd* B	*Gpi* C	*Pgm-1* D	*Idh-2* A	*Sod-3* B	*6Pgd* C	*Idh-1* B	*Mdh-1* B	*Mdh-2* A	*Sod-1* B	*Sod-2* A
S1	0.839	0.452	0.894	0.666	—	—	1.000	0.983	1.000	0.991	—	—
S2	0.793	0.384	0.878	0.444	—	—	0.945	0.990	1.000	1.000	—	—
S3	0.618	0.433	0.970	0.530	—	—	0.978	0.996	0.996	1.000	—	—
S4	0.789	0.513	0.924	0.607	—	—	—	—	—	—	—	—
S5	0.779	0.547	0.860	0.474	—	—	0.959	1.000	0.985	1.000	—	—
S6	0.672	0.394	0.743	0.515	0.950	0.786	0.965	1.000	1.000	1.000	0.989	1.000
C1	0.750	0.520	0.900	0.460	0.960	1.000	1.000	1.000	0.990	1.000	1.000	1.000
C2	0.790	0.410	0.880	0.570	0.950	0.930	1.000	0.990	0.980	1.000	1.000	1.000
C3	0.648	0.385	0.900	0.516	0.943	0.691	1.000	0.959	1.000	0.992	1.000	1.000
C4	0.721	0.380	0.836	0.568	0.913	0.858	1.000	0.990	1.000	0.990	1.000	1.000
C5	0.650	0.340	0.869	0.565	0.945	0.738	0.995	1.000	1.000	1.000	0.990	1.000
C6	0.690	0.330	0.855	0.601	0.950	0.601	1.000	0.990	1.000	1.000	1.000	1.000
C7	0.765	0.428	0.842	0.618	0.902	0.837	0.975	0.990	0.995	1.000	1.000	1.000
RN1	0.700	0.400	0.880	0.580	0.940	0.970	0.990	1.000	0.990	1.000	1.000	1.000
RN2	0.800	0.650	0.870	0.680	0.940	0.990	0.990	0.990	0.990	1.000	1.000	1.000
RN3	0.854	0.530	0.839	0.580	—	—	0.980	—	1.000	—	—	—
RN4	0.630	0.610	0.890	0.550	0.960	0.930	1.000	0.970	0.990	1.000	1.000	1.000
RN5	0.840	0.525	0.875	0.575	0.930	0.975	0.990	1.000	0.980	1.000	1.000	1.000
RN6	0.785	0.460	0.925	0.535	0.905	0.965	0.985	0.990	0.985	1.000	1.000	1.000
RN7	0.827	0.460	0.894	0.550	0.895	0.961	0.972	1.000	0.994	1.000	0.994	1.000
RN8	0.815	0.580	0.935	0.635	0.935	0.975	0.990	0.985	1.000	1.000	1.000	1.000
RN9	0.790	0.590	0.920	0.580	0.940	0.970	0.960	0.990	1.000	1.000	1.000	1.000
RN10	0.820	0.440	0.940	0.560	0.900	0.960	0.960	0.980	0.980	0.990	1.000	1.000
RN11	0.880	0.570	0.920	0.690	0.960	0.940	0.990	0.970	1.000	1.000	1.000	1.000
RN12	0.783	0.454	0.914	0.566	—	—	0.959	0.990	0.995	1.000	—	—
RN13	0.748	0.545	0.910	0.552	—	—	0.985	0.995	0.990	1.000	—	—
RN14	0.807	0.491	0.915	0.697	—	—	0.960	1.000	1.000	0.996	—	—
RN15	0.823	0.479	0.958	0.614	—	—	0.995	0.995	0.990	0.995	—	—
RN16	0.781	0.619	0.865	0.635	0.906	—	0.969	1.000	1.000	1.000	—	—
RN17	0.775	0.390	0.830	0.560	0.895	—	0.980	0.995	0.990	1.000	—	—
RN18	0.850	0.417	0.917	0.650	0.967	0.917	1.000	0.983	1.000	1.000	1.000	1.000
RN19	0.867	0.466	0.837	0.645	—	—	0.985	—	1.000	1.000	—	—
RN20	0.864	0.444	0.850	0.677	—	—	0.990	—	1.000	1.000	—	—
RN21	0.753	0.338	0.864	0.572	—	—	0.995	—	1.000	—	—	—
RN22	0.732	0.418	0.854	0.531	—	—	0.995	—	0.995	1.000	—	—
RN23	0.714	0.475	0.820	0.490	—	—	0.990	—	0.990	1.000	—	—
RN24	0.715	0.429	0.874	0.582	—	—	0.960	—	0.990	0.995	—	—
Average	0.769	0.467	0.885	0.579	0.933	0.894	0.983	0.990	0.994	0.999	0.999	1.000
Fst	0.027	0.027	0.018	0.016	0.009	0.136	0.015	0.011	0.008	0.007	0.009	—

Mean — : not examined

0.894 and Fst was 0.136. At the *6Pgd* locus, four alleles were detected and the *C* allele was dominant. The frequency of *C* allele ranged from 0.945 to 1.000 with a mean of 0.983 and Fst was 0.015. These three loci, *Idh-2*, *Sod-3* and *6Pgd* showed polymorphism in 17 of the 21 lots, in 10 of the 19 lots, and 1 of the 36 lots examined, respectively.

At the *Idh-1* locus, rare variants were observed in 20 of 29 lots examined. At the *Mdh-1* and *Mdh-2* loci, rare variants were observed in 19 of 36 lots and 7 of 35 lots examined, respectively. *Sod-1* and *Sod-2* loci were monomorphic in all or almost all lots examined.

The degree of genetic fluctuation among lots measured by Fst shows that the genetic constitution of samples was not uniform. The difference among collecting years in the same location was larger than that among collecting locations.

Excess of Homozygosity

Four polymorphic loci, *Aat-1*, *αGpd*, *Gpi*, and *Pgm-1* were used for the calculation of heterozygosity. Table 3 gives the observed and expected heterozygosity in each lot. The observed heterozygosity was lower than the expected heterozygosity in 25 of the 37 lots at the *Aat-1*, in 30 of the 37 lots at the *αGpd*, in 24 of the 37 lots at *Gpi*, and in 21 of the 37 lots at the *Pgm-1* locus. A significant deviation from the the expected heterozygosity was observed at the *Aat-1*, *αGpd*, and *Pgm-1* but not observed at the *Gpi*. This indicates that the excess of homozygosity varied from locus within lots and the locus-specific excess also varied between lots. The value measured by (Ho−He)/He for 4 loci showed the excess of homozygosity tends to be significant in all lots from seed population but not significant in most lots from the cultured population and released and natural population.

Change of Homozygote Excess during Growth

In order to elucidate the relation between homozygote excess and size, correlation of *d* value measured by (Ho−He)/He was examined with the mean and coefficient of variance in shell length of each lot. The results are shown in Figs. 1 and 2. A positive correlation was observed between the *d* value and the mean of shell length. This indicates that a decrease of homozygosity is accompanied with the growth (age). A negative correlation was observed between the *d* value and the coefficient of variance in shell length. This indicates that a decrease of homozygosity is associated with the decrease of variance in the shell length.

To identify whether the correlation exists dependently or independently among isozyme loci, correlation coefficients (r) of the *d* value with mean and variance in the shell length were calculated at each locus (Table 4). A significant correlation was observed at *αGpd* and *Gpi* loci in the mean of shell length and was

TABLE 3 *Observed and Expected Heterozygosity and D value at 4 loci in Japanese Scallop*

	Aat-1			*αGpd*			*Gpi*		
Lot	Ho	He	D	Ho	He	D	Ho	He	D
S1	0.322	0.277	+0.162	0.351	0.590	−0.405*	0.177	0.191	−0.073
S2	0.333	0.347	−0.040	0.495	0.643	−0.230*	0.204	0.215	−0.051
S3	0.307	0.472	−0.350*	0.527	0.637	−0.173*	0.043	0.058	−0.259
S4	0.353	0.333	+0.060	0.487	0.567	−0.141	0.136	0.140	−0.029
S5	0.361	0.360	+0.003	0.474	0.588	−0.194*	0.198	0.243	−0.185
S6	0.402	0.470	−0.145	0.436	0.497	−0.123	0.354	0.387	−0.085
Ave	0.346	0.377	−0.051	0.462	0.587	−0.211	0.185	0.206	−0.114
C1	0.380	0.400	−0.050	0.460	0.551	−0.165	0.160	0.180	−0.111
C2	0.300	0.343	−0.125	0.520	0.568	−0.085	0.160	0.213	−0.249
C3	0.410	0.462	−0.113	0.443	0.493	−0.101	0.167	0.180	−0.072
C4	0.462	0.415	+0.113	0.540	0.513	+0.053	0.308	0.276	+0.116
C5	0.380	0.455	−0.165	0.505	0.482	+0.048	0.182	0.228	−0.202
C6	0.430	0.431	−0.002	0.420	0.517	−0.188	0.190	0.248	−0.234
C7	0.398	0.384	+0.036	0.557	0.600	−0.072	0.235	0.266	−0.117
Ave	0.394	0.413	−0.044	0.492	0.532	−0.073	0.200	0.227	−0.124
RN1	0.440	0.431	+0.021	0.640	0.620	+0.032	0.200	0.213	−0.061
RN2	0.320	0.335	−0.045	0.460	0.511	−0.100	0.220	0.226	−0.027
RN3	0.253	0.251	+0.008	0.505	0.553	−0.087	0.232	0.276	−0.159
RN4	0.340	0.478	−0.281	0.480	0.528	−0.091	0.220	0.196	+0.122
RN5	0.240	0.270	−0.111	0.600	0.581	+0.033	0.210	0.220	−0.045
RN6	0.290	0.338	−0.142	0.550	0.585	−0.060	0.150	0.139	+0.079
RN7	0.278	0.290	−0.041	0.544	0.603	−0.098	0.167	0.190	+0.121
RN8	0.350	0.302	+0.159	0.530	0.551	−0.038	0.110	0.122	−0.098
RN9	0.260	0.336	−0.226*	0.620	0.527	+0.176	0.160	0.147	+0.088
RN10	0.240	0.295	−0.186	0.600	0.573	+0.047	0.120	0.113	+0.062
RN11	0.240	0.213	+0.127	0.420	0.543	−0.227	0.160	0.149	+0.074
RN12	0.320	0.335	−0.045	0.460	0.511	−0.100*	0.220	0.226	−0.027
RN13	0.323	0.384	−0.159	0.515	0.548	−0.060	0.160	0.164	−0.024
RN14	0.226	0.317	−0.287*	0.525	0.582	−0.098	0.137	0.156	−0.122
RN15	0.292	0.295	−0.010	0.553	0.590	−0.063	0.063	0.080	−0.213
RN16	0.271	0.342	−0.208	0.478	0.487	−0.018	0.271	0.236	+0.148
RN17	0.380	0.364	+0.044	0.520	0.594	−0.125	0.300	0.287	+0.045
RN18	0.300	0.255	+0.176	0.533	0.557	−0.043	0.167	0.152	+0.099
RN19	0.223	0.232	−0.039	0.489	0.558	−0.124	0.265	0.273	−0.029
RN20	0.212	0.235	−0.098	0.541	0.559	−0.032	0.280	0.255	+0.098
RN21	0.374	0.374	0	0.475	0.461	+0.030	0.232	0.235	−0.013
RN22	0.371	0.392	−0.054	0.485	0.521	−0.069	0.253	0.249	+0.016
RN23	0.408	0.414	−0.014	0.545	0.547	−0.004	0.300	0.297	+0.010
RN24	0.310	0.408	−0.240*	0.525	0.538	−0.024	0.253	0.220	+0.150
Ave	0.303	0.328	−0.069	0.525	0.551	−0.048	0.202	0.200	+0.002
Total Ave	0.327	0.352	−0.061	0.508	0.553	−0.079	0.199	0.207	−0.040

TABLE 3 *continued*

	loci					
	Pgm-1			Ave. of 4 loci		
Lot	Ho	He	D	Ho	He	D
S1	0.470	0.502	−0.064	0.330	0.390	−0.154
S2	0.545	0.661	−0.175*	0.394	0.467	−0.156
S3	0.470	0.626	−0.249*	0.337	0.448	−0.248
S4	0.607	0.556	+0.092	0.396	0.399	−0.008
S5	0.417	0.579	−0.280*	0.362	0.443	−0.183
S6	0.660	0.581	+0.136	0.463	0.484	−0.043
Ave	0.528	0.584	−0.090	0.380	0.439	−0.132
C1	0.660	0.659	+0.002	0.415	0.448	−0.074
C2	0.560	0.587	−0.046	0.385	0.428	−0.100
C3	0.607	0.609	−0.003	0.406	0.436	−0.069
C4	0.476	0.541	−0.120	0.446	0.436	+0.023
C5	0.580	0.550	+0.055	0.412	0.429	−0.040
C6	0.505	0.527	−0.042	0.386	0.431	−0.104
C7	0.612	0.557	+0.099	0.450	0.452	−0.004
Ave	0.571	0.576	−0.008	0.414	0.437	−0.053
RN1	0.520	0.577	−0.099	0.450	0.461	−0.024
RN2	0.580	0.494	+0.174	0.395	0.392	+0.008
RN3	0.545	0.581	−0.062	0.384	0.415	−0.075
RN4	0.640	0.629	+0.017	0.420	0.457	−0.081
RN5	0.640	0.574	+0.115	0.423	0.411	+0.029
RN6	0.630	0.597	+0.055	0.405	0.415	−0.024
RN7	0.678	0.607	+0.117	0.417	0.422	−0.012
RN8	0.540	0.524	+0.031	0.383	0.375	+0.021
RN9	0.600	0.583	+0.029	0.410	0.398	+0.030
RN10	0.640	0.585	+0.094	0.400	0.392	+0.020
RN11	0.460	0.481	−0.044	0.320	0.346	−0.075
RN12	0.449	0.549	−0.182*	0.346	0.415	−0.166
RN13	0.567	0.592	−0.042	0.391	0.422	−0.073
RN14	0.410	0.473	−0.133	0.324	0.382	−0.152
RN15	0.527	0.545	−0.033	0.359	0.377	−0.048
RN16	0.500	0.518	−0.035	0.380	0.396	−0.040
RN17	0.550	0.603	−0.088	0.438	0.462	−0.052
RN18	0.433	0.516	−0.161	0.358	0.370	−0.032
RN19	0.557	0.517	+0.077	0.384	0.395	−0.028
RN20	0.556	0.487	+0.142	0.397	0.384	+0.034
RN21	0.510	0.559	−0.088	0.398	0.407	−0.022
RN22	0.582	0.596	−0.023	0.422	0.440	−0.041
RN23	0.596	0.599	−0.005	0.462	0.464	−0.004
RN24	0.577	0.566	+0.019	0.416	0.433	−0.039
Ave	0.554	0.556	−0.005	0.395	0.410	−0.035
Total Ave	0.553	0.565	−0.019	0.396	0.420	−0.054

* : Significant difference between Ho and He at each 4 locus

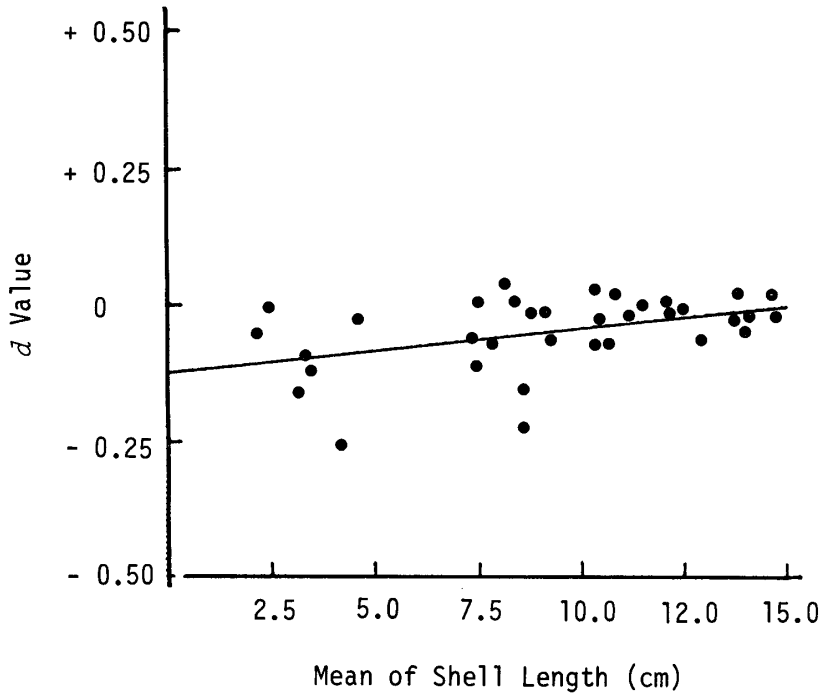

FIG. 1. Relationship betweed the d value measured by (Ho−He)/He and the mean of shell length of Japanese scallop.

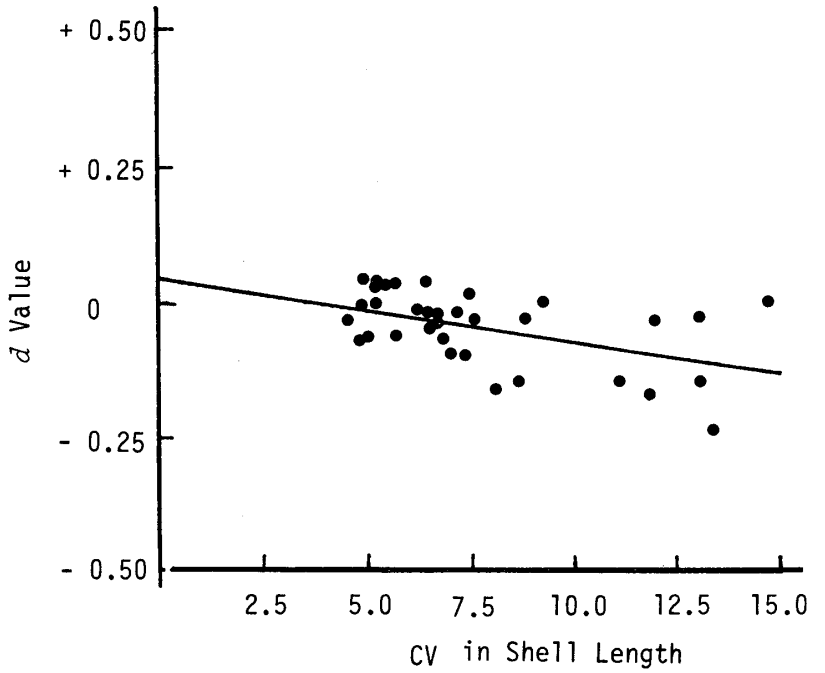

FIG. 2. Relationship between the d value measured by (Ho−He)/He and the CV of shell length in the lots of Japanese scallop.

TABLE 4 *Correlation coefficient(r) between the d value measured by (Ho−He)/He and Mean and the coefficient of variation (CV) in the shell length (N=37)*

	Mean	Coefficient of variance
Overall 4 loci	+0.432**	−0.487**
Aat-1	−0.037	+0.155
α-Gpd	+0.538**	−0.515**
Gpi	+0.330*	−0.181
Pgm-1	+0.246	−0.382*

*: $P<0.05$ **: $P<0.01$

also observed at *αGpd* and *Pgm-1* loci in the coefficient of variance. A decrease of homozygosity during the growth was observed at the *αGpi*, *Gpi* and *Pgm-1* loci but was not observed at the *Aat-1* locus. The meaned shell lengths of homozygotes and heterozygotes in each lot were compared at the *Aat-1*, *αGpd*, *Gpi* and *Pgm-1* loci. The difference between homozygotes and heterozygotes was not significant.

Discussion

The level of genetic variation in the Japanese scallop population is high as deduced from the present study on protein polymorphism. Fujio *et al.* (5) have demonstrated that marine molluscs are generally more variable than marine teleosts and revealed that the frequency of homozygotes were significantly higher than those expected under Hardy-Weinberg's equilibrium in natural population in most of pelecypodes with pelagic larvae. In the present study, a significant homozygote excess was demonstrated at the *αGpd*, *Gpi* and *Pgm-1* loci in the seed (small size) population. Preliminary data shows that the smallest seed scallops in the collectors of Abashiri and Mutsu Bay have a high level of homozygote excess ($d=-0.061$ in Abashird and $d=-0.103$ in Mutsu Bay) at the *Pgm-1*. These seeds are the origin of S4 and S6 lots which did not show the homozygote excess. The simplest explanation is that this generalized homozygote excess over the genome results from the breeding structure of the population.

The "Wahland effect" has been proposed as a general explanation of this homozygote excess observed in pelecypode with free swiming larvae by Tracey *et al.* (6). The "Wahland effect" is expected to affect the loci at which the difference of allele frequency is significant between subpopulations. The Fst suggests that the seed population structure consists of a number of larval populations of different parental origins that produce patchness. Such circumstances are supported by the genetic differentiation observed among localities of adult scal-

lops on the Okhotsk Sea coast of Hokkaido in Japan (1). The mixture might be due to the great dispersal distance of the pelagic larvae.

The present study has demonstrated a decrease of homozygosity during growth (age) of the Japanese scallop. However, size difference between homozygotes and heterozygotes was not observed in each lot. Thus, a decrease of homozygosity during the growth can be explained by the hypothesis that heterozygotes at the isozyme loci are positively correlated to viability and survival but not growth, probably on the basis of homozygosity of deleterious recessive allele linked with isozyme loci. In this context, evidence suggesting inbreeding structure and overdominance in wild and cultured populations of the Pacific oyster (*Crassostrea gigas*) was presented by Fujio *et al.* (7), who observed a homozygote excess at the *Idh-1* locus and heterozygote excess at the *Cat* locus associated with survival rate. In the cultured population of apple snail (*Pomacea canaliculata*), the hatchability per egg lump was found to be lower when the possibility of heterozygotic pairs of chromosome was 50 per cent, compared to a 75 per cent level. This suggested an apparent advantage of heterozygotic pairs of chromosome in hatchability (8).

Moreover, Fujio *et al.* (9) revealed homozygote excess in some natural Pacific abalone (*Haliotis discus hannai*) populations and reported that populations showing high homozygote excess also tended to show a wide range in soft part weight/whole body weight, while populations showing no homozygote excess showed a narrow range. These results are interpreted as being a reflection of the effect of both harmful and advantageous alleles in homozygote state.

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